



Differential acoustic response specificity and directionality in the round goby, *Neogobius melanostomus*

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The ability to differentiate and localize conspecific calls from the ambient soundscape is particularly challenging for aquatic animals because of the increased wavelength, and concomitant increased distortion, of sound underwater. The increased wavelength is especially problematic for fish because of the relatively small space between their two ears, making interaural comparisons difficult. We presented round goby with conspecific calls, two heterospecific calls (*Padogobius bonelli* and *Gobius niger*), white noise and a 100 Hz tone burst to ascertain the effects of sound structure on localization abilities. The round goby has no obvious hearing specializations, causing theory to predict that it should not be able to localize sounds. In the laboratory, fish were presented with a silent speaker and a speaker playing one sound of interest and their behavioural response was quantified. In all trials except those using *Gobius niger* calls, fish preferentially selected the playing speaker over the silent but the intensity of this response differed with sound type. When the round goby call was played, fish came closer to the speaker and swam faster when responding. Also, the ability to directionalize the sound, measured by examining the path taken to the speaker, was significantly better when the conspecific call was played than when other sounds were presented. While it is still unclear how the round goby is able to directionalize the conspecific call, it appears clear they can directionalize, and possibly localize, conspecific calls as well as differentiate between call types.

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For an animal to effectively use acoustic signals in mating, at least some members of the species must be able to produce and respond to sounds, directionalize sound sources and differentiate between conspecific, heterospecific and background signals to segregate different portions of the 'auditory stream' (Fay 1998; Moss & Surlykke 2001; Schul & Sheridan 2006). This combination of attributes has been clearly shown in many vertebrates (e.g. Bradbury & Vehrencamp 1998; Phelps et al. 2006) but it is less well documented in fishes, the most speciose group of extant vertebrates. Many fish species produce sounds in reproductive displays (reviewed in Ladich 2004), and playback experiments in a few species have shown an attractive function of these calls (e.g. Gerald 1971; Myrberg &

Spires 1972; Lugli et al. 1996; McKibben & Bass 1998). Fish have been shown to be more attracted to conspecific than heterospecific calls (Delco 1960; Myrberg & Spires 1972; Myrberg et al. 1986) and may be able to differentiate sounds based on call structure (McKibben & Bass 1998; Lugli et al. 2004), showing the potential importance of sound as an effective signal. Numerous issues remain unresolved, however, especially how fish can directionalize these sounds and how conspecific preference might have evolved in the first place (Ryan & Rand 1993). Understanding of these issues is necessary to fully appreciate how acoustic displays are used in fish and how they evolved in vertebrates in general.

The ability to localize sound is probably one of the most fundamental aspects of the auditory system (Masterton & Imig 1984; Fay 2005). Terrestrial vertebrates perform localization through a combination of interaural time and intensity differences to extract precise

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directional information in the brain (Oswald et al. 1999; Hancock & Delgutte 2004). Given that the speed of sound is about five times higher in water than in air, and the distance between the two ears in fish is generally no more than a few centimetres, fish cannot use interaural time, phase and intensity differences of sound pressure to localize a sound source (van Bergeijk 1967; Fay & Feng 1987). Despite this, fish have been shown to find sound sources (e.g. Popper et al. 1973; Schuijf & Siemelink 1974; McKibben & Bass 1998; Tolimieri et al. 2000; Rollo et al. 2007) although debate remains on whether this is true sound localization; defined here as being able to go directly to the sound from a distance as opposed to sampling different parts of the acoustic field and following sound gradients (Fay 2005).

Current models of fish hearing assume that fish determine the direction of incident sound through otolith motion along the direction of the acoustic wave (de Vries 1950; Fay 1984, 2005; Lu et al. 1996). The complex geometry of fish otoliths and differential hair cell polarity may help to distinguish sound flow patterns from different directions (Popper & Coombs 1982; Lu & Popper 2001). Cod, *Gadus morhua*, have the ability to orient towards a sound source under free-field conditions (Schuijf 1975) and can discriminate between sources separated by 10–20° in azimuth, as well as sources from opposing directions (180° apart) in both the horizontal and vertical planes (Schuijf & Buwalda 1975). It has been argued that only fish with a swim bladder should be able to differentiate sounds coming from opposite directions (Schuijf 1975; Schuijf & Buwalda 1975; Rogers et al. 1988) but some species that lack a swim bladder seem to show sound source directionality (Tavolga 1958; Lugli et al. 1996; Myrberg & Stadler 2002) and perhaps localization (Rollo et al. 2007). How fish perform these functions, and what effects different sorts of signals have on directionality and localization, remains a mystery but understanding these concepts is vitally important to understanding the evolution of auditory signalling.

We examined round gobies' directional response abilities to conspecific spawning cues and their response specificity to conspecific versus heterospecific vocalizations. Round gobies have no swim bladder or other obvious hearing specializations and yet use sound for reproductive communication (Protasov et al. 1965; Rollo et al. 2007). Many species in the Gobiidae, the family to which round gobies belong, produce and react to auditory cues (Tavolga 1956; Lindström & Lugli 2000; Lugli et al. 2004), primarily in a reproductive context. Round gobies in particular and gobiids in general often live sympatrically with other vocalizing species, making evolution of sound discrimination necessary for effective use of reproductive calls. The mechanisms of this discrimination ability remain unclear and yet are an integral part of understanding how auditory signalling has evolved in an often noisy environment. The current study used playback of natural spawning sounds of three Gobiidae species and two synthetic sounds to examine differential behavioural specificity and acoustic directionality in free-swimming round gobies.

METHODS

Housing Conditions

Fish used in these experiments were collected by angling at different shoreline sites from the Detroit River and Lake Erie. After capturing 10–20 gobies (time frame 30–60 min), they were transported to the laboratory, approximately 10–30 min away. In the laboratory, the gobies were housed temporarily in the transport container equipped with an airstone, until transferred to the experiment tank. Animals were not returned to the wild after experiments because of the invasive nature of this species (Charlebois et al. 1997). All experimental procedures complied with University of Windsor Animal Care regulations.

Experimental Set-up

Behavioural experiments were conducted in a 1020-litre rectangular (240 × 92 cm, L × W) fibreglass tank with dechlorinated tap water (water depth = 33 cm). At one end of the tank were two underwater speakers (UW-30, Lubell Labs, Columbus, OH, U.S.A.) suspended from the ceiling of the room so as not to contact the sides or bottom of the tank. The speakers were connected to an amplifier (Alesis RA300, Alesis Inc., Santa Monica, CA, U.S.A.), which was in turn connected to a laptop computer. One speaker was designated the 'active' speaker (playing the experimental sounds) and one the 'quiet' speaker (no sound being played), with the speakers placed 41 cm apart (centre to centre). The order of presentation alternated sequentially between the two speakers from trial to trial, and each fish was used only once, so no a priori knowledge of speaker position was possible. The tank was divided by a mesh net, 107 cm from the speakers. Gobies were placed on the speaker side of the mesh to begin trials. This allowed placement of the goby at a defined distance from the speaker. The net also kept the gobies at least 108 cm from the back of the tank, thus limiting the gobies' exposure to reverberations. While it was not possible to directly measure the amount of reverberation in the tank, sound level decreased from the net towards the back of the tank (Fig. 1). This suggests that reverberation was not a significant problem in the current study, although there was some reradiation of sound from the sides of the tank (Fig. 1a, b). To begin an experiment, one goby was placed into the experimental tank with the experimental sound starting immediately afterward. There was no acclimation period owing to the goby's limited response time once brought into the laboratory (responsiveness to sounds decreased after fish had been held in the laboratory for over 2 h). The decibel level (as measured by a precalibrated hydrophone, InterOcean Inc., San Diego, CA, U.S.A.) and particle acceleration (estimated from the pressure gradient between two hydrophones; see below) of the sound stimulus in the experimental tank varied slightly depending on sound stimulus presented (specific ranges are below). The experiment ended when a response was observed from the goby, or 10 min had elapsed. The goby was then removed and the sex was determined by examination of the urogenital papillae.

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